CHAPTER 5-3

Functions of the Vestibular System in Human Guidance and Control

L. R. Young

Summary

A physical analog model of the vestibular system was developed for research purposes. The model consists of a three-gimbal "head" containing three rate gyroscopes and six linear accelerometers, and a special purpose analog computer simulating the dynamics and nonlinearities of the non-auditory labyrinth.

The vestibular package can be rotated through normal head movements by the machine and mounted on a centrifuge or flown to measure actual motion inputs. The distance between the "ears" is adjustable, as well as the orientation of the sensitive direction of each canal and otolith axis. The computer console permits adjustment of the important gains, nonlinearities and time constants of the vestibular system for utility in refining models, training physiologists, predicting orientation perception or nystagmus and for aids in design of moving base simulators or artificial g platforms.

Functions of the Vestibular System in Human Guidance and Control

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Introduction

The non-auditory labyrinth represents a remarkable set of biological transducers which permit man to control his posture, direct his gaze and perceive his orientation with respect to the external world. This vestibular mechanism has been of particular interest to engineers, scientists and physicians associated with aerospace medicine for two reasons. The troublesome aspects of vestibular responses concern the illusions which pilots and passengers may experience in unusual environments, leading to possible disorientation, vertigo and motion sickness. The problems of bizarre vestibular stimulation associated with extended space flight with or without artificial gravity have been explored at length. The non-auditory labyrinths also represent a significant challenge and opportunity for bionics exploration. As a short period attitude sensor package, the vestibular system is at once miniature, reliable, simple, rapidly responding and with static and dynamic ranges admirably suited to its task of sensor for attitude stabilization.

The non-auditory labyrinth in each inner ear consists of sets of semicircular canals and otoliths. The three semicircular canals oriented in roughly orthogonal planes respond to angular accelerations along an axis normal to the plane of each canal. The otoliths are stimulated by linear acceleration as well as the gravity field and they are analogous to 3-axis accelerometer packages. An engineer familiar with inertial navigation systems is tempted to draw the analogy, with the semicircular canals providing attitude signals usually generated by gyroscopes, and the otoliths providing the specific force signals twice integrated to yield position. Although man seems to lack the accurate low drift integrators required for this type of navigation, the nonvisual perception of position in space is computed by this system.

An additional important function of the vestibular system is the stabilization of the eye with respect to the external visual field via the mechanism of vestibular nystagmus. By response to signals from the semicircular canals and probably the otoliths, the eyes are driven with an angular velocity opposite that of the head. At frequent intervals in the process of nystagmus, the eyes are rapidly slewed to a new position whereupon they resume their slow rotation which tends to stabilize the image on the retina. An immediate analogy may be drawn to the problem of stabilization of a star tracker, camera or fire control system from a moving base.

This paper documents the first physical analog model of the entire vestibular system. The model is based on our current knowledge of the functioning of the vestibular apparatus. It will enable investigators to predict the vestibular responses to a variety of motion inputs, thereby predicting possible problem areas for flight situations, suggesting physiological experiments to refine the model and hopefully inspire the development of further mechanical systems employing some of the desirable characteristics of the human non-auditory labyrinth.

The vestibular model, like the human or animal ear, accepts as its inputs actual physical motions which are sensed by inertial transducers, processed by a special purpose computer and presented in the form of subjective responses or nystagmus velocity.

The physical model consists of two major subassemblies: a 3-axis gimbal system which simulates head motion and supports the inertial transducers, and a special purpose analog computer console which provides for signal conditioning and simulation of the vestibular system dynamics. Each of these subassemblies is independent and self-contained.

The head motion simulator is composed of a 3-axis gimbal assembly which can be driven to a desired head position and inertial sensors which substitute for the human biological sensors (canals and otoliths). Inputs to both the left and right canals are simulated by a single 3-axis rate gyro package. (Under the assumption of a rigid skull, both ears are always subject to the same angular velocity.) The left and right otoliths are simulated by two 3-axis linear accelerometer arrays. Two of the accelerometers are mounted so that the spacing between them is adjustable. This feature allows for simulation of differences in the head geometries of men and the various experimental animals. The entire gimbal subassembly is self-contained, portable and rugged. The gimbal assembly, therefore, is suitable for experiments conducted on board a maneuvering aircraft or on a centrifuge.

The head motion simulator, shown in figure 5-3-1, was modified from an inertial guidance package developed at the Massachusetts Institute of Technology (M.I.T.). The analog computer subassembly contains all of the operating controls, computer elements, signal conditioning circuitry, test equipment and power supplies necessary to complete the desired vestibular simulation. This assembly includes 82 operational amplifiers, 52 front panel precision potentiometers, a number of operating switches, both an analog and a digital voltmeter, power supplies and many other components. These elements are contained in a desk-top console cabinet shown in figure 5-3-2.

Mathematical Model of Vestibular Function

Derivation of mathematical models for semicircular canal and otolith functions has entailed extensive physiological and behavioral experiments on men and animals. The continuing development of these models provides an interesting story of the interplay among engineers, physiologists and psychologists. The current state of biocybernetic models as developed at M.I.T. is reviewed in ref. (1) and summarized in the block diagram of figure 5-3-3.

The inputs to the model are the angular velocity and specific force (gravity minus acceleration) of the head with respect to inertial space. We can consider coordinates of these vectors in head fixed axes: sagittal (pitch), lateral (roll) and vertical (yaw). To express each of the components as a component along the axes normal to each canal or along the sensitive axes of the otoliths requires a fixed matrix coordinate transformation.

Components of angular velocity are then processed by the "canal dynamics," which are different for the vertical canals (posterior and superior) than for the horizontal canals of each ear.

Despite several points of disagreement with experimental evidence, the prevalent mathematical model for the semicircular canals is essentially the overdamped torsion pendulum model based on the work of Van Egmond, Groen and Jongkees (2) interpreting the earlier experiments of Steinhausen. For this model, the semicircular canal is viewed as a simple second-order mechanical system acting as an overdamped angular accelerometer. The moment of inertia of the fluid ring in the canal creates an inertial reaction force when the skull is rotated and tends to lag

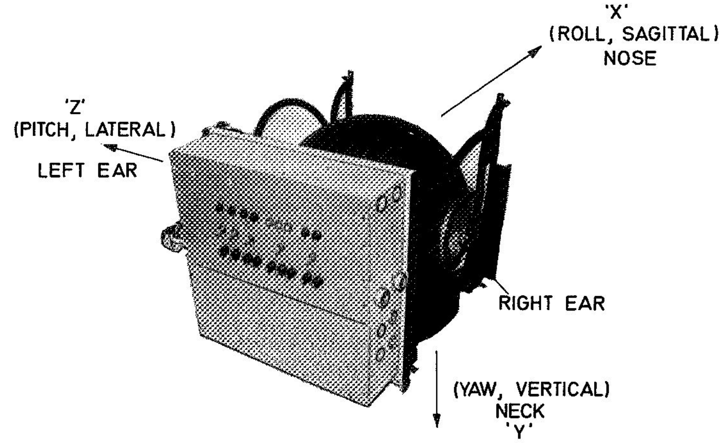

Fig. 5-3-1 Head motion simulator

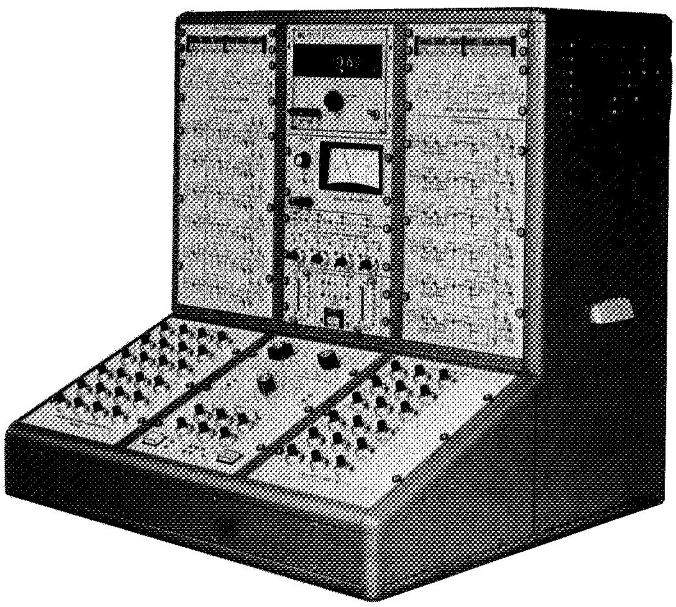

Fig. 5-3-2 Vestibular model console

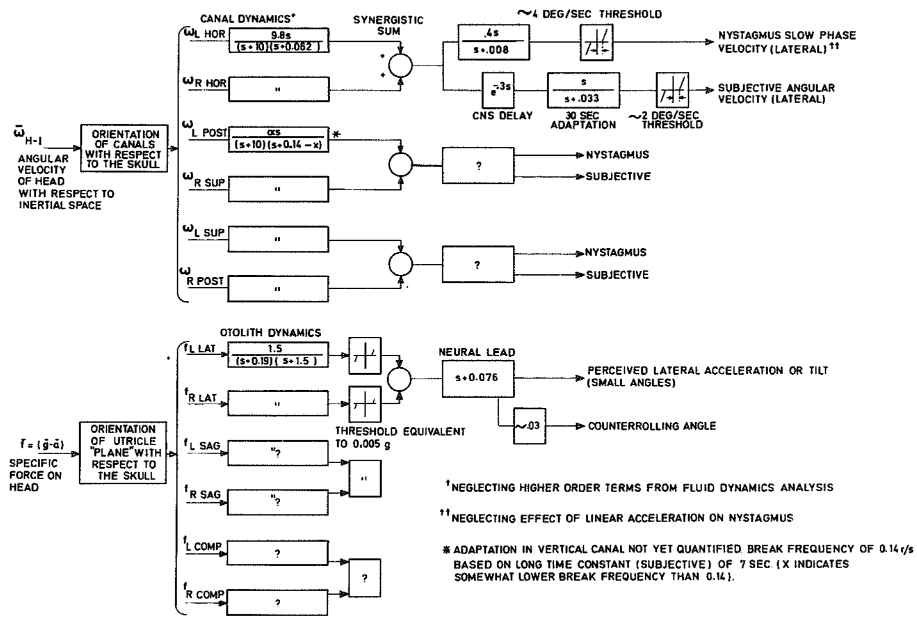

Fig. 5-3-3 Summary diagram. Biocybernetic model of the vestibular system, 1968

behind the membranous labyrinth. The damping term is attributable to viscous forces relating to flow of endolymph through the canal and, it was recently suggested, the friction associated with movement of the cupula along the ampulla (3). The elastic restraining force of the cupula tends to return it to its neutral position whenever it has been displaced by any movement of endolymph. The angular deviation of the cupula is taken as the output signal of the semicircular canal. The cupula and crista form a type of flapper valve to detect motion of endolymph. The crista contains hair-like sensory cell endings which change their firing rate upon bending. When angular accelerations of the head cause the endolymph fluid to lag behind the canal structure, the cupula is displaced from its normal position and the change is signaled by a change in firing rate of the vestibular nerve.

Because of the low moment of inertia to damping ratio and low spring constant, the semicircular canals are extremely overdamped angular accelerometers and they transduce angular velocity in the normal physiological frequency range of 0.1 to 10 radians/sec.

The attempts to establish the values of time constants based on fluid dynamics analysis of the semicircular canals have only been partially successful, although Steer recently showed that using a rigorous analysis for the rigid torus the higher order terms are negligible compared to the dominant damping term associated with the simple torsion pendulum model (3).

A transfer function relating cupula deflection to angular velocity of the skull is:

$$\frac{\text{cupula deflection}}{\text{skull velocity}} = \frac{bs}{(s + a)\ (s + b)}$$

$$s = jw = j2\pi \text{ frequency}$$

Table 5-3-1 Canal Transfer Function Coefficients

	Nominal	Min.	Max.	Parameter
a	0.062	0.04	1.0	low freq. break, rad/sec
b	10.0	0	300.0	high freq. break, rad/sec

The break frequencies a and b are associated with the two dominant time constants of the system. The lower break frequency (a) is associated with the long time constant characterizing the slow return of the cupula to its neutral position by the elastic restoring force acting against the viscous damping. The upper break frequency (b) is associated with the rapid time constant for the cupula position to respond to angular acceleration, as the viscous damping torque quickly equilibrates the inertial reaction torque associated with accelerating the ring of endolymph. The outputs of the canals from the two ears are assumed to be combined in a "synergistic sum," which can be taken simply as the average of the two signals.

Our recent investigations of the adaptation phenomenon, or decreased sensitivity to prolonged accelerations, shows that many previously paradoxical results are explained by the inclusion of simple first order adaptation operators with long time constants (4). The adaptation function is not currently included in the physical model but is easily added. The operators serve to shift the reference level for angular velocity.

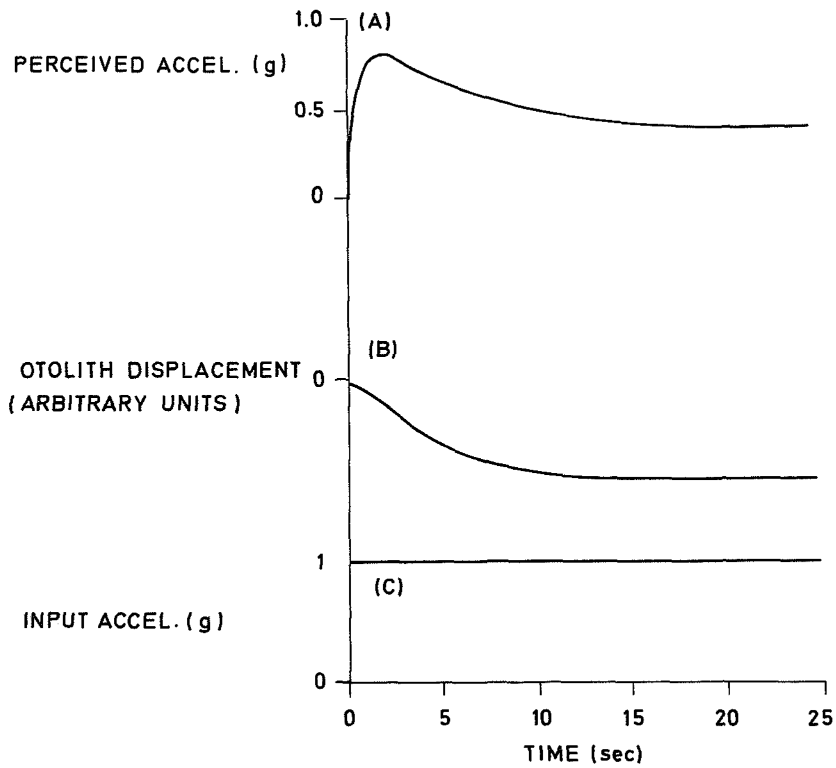

Fig. 5-3-4 Step responses of linear model:
(A) perceived acceleration of tilt
(B) otolith displacement
(C) acceleration or tilt step input

Finally, the semicircular canal response is seen to exhibit a threshold phenomenon in both subjective velocity and nystagmus.

In marked contrast to the wealth of experimental evidence available to check the models of the semicircular canals, until recently almost no quantitative data on the dynamic responses of the otoliths was available. Even the question of what the stimulus to the otolith was, has been open to some question.

The utricle, or large oblong sac in the vestibule, is the site of one of the two otoliths responsible for detecting linear acceleration and orientation with respect to gravity. (The other otolith of somewhat obscure function is located in the saccule). The otolith is a gelatinous mass with heavy calcium carbonate grains embedded in it and is partially floated in endolymph. Although the otoliths and the macula beneath them are not strictly planar, a principal plane can be determined. Current theories of otolith operation involve detection of the displacement of "seismic mass" or otolith, with respect to the fixed macula, upon stimulation by specific force components in the plane of the otolith. Bending of the hair cells from the macula which support the otolith serves to indicate the otolith displacement and is used for sensation of orientation with respect to the vertical. The utricular otolith is highly sensitive to changes in direction of specific gravity and less so to changes in its magnitude.

Otolith responses are believed to provide the primary non-visual cue regarding orientation to the "vertical" and they are of considerable importance in postural control.

The current otolith models shown in figure 5-3-3 resulted from a variety of linear acceleration tests at M.I.T. (5), (6). Only the lateral and sagittal axes have been explored, with these axes defined in the plane of the utricle which is elevated 30 degrees from the horizontal about the lateral axis. Dynamic characteristics in the third "compressive" axis are still unknown. The mechanical dynamics of the otolith are modeled as a highly overdamped linear accelerometer, with a light mass and weak restraining "spring". Following a threshold element corresponding to a dead zone of 0.005 g's, a term corresponding to "neural lead" has been included. This latter term reflects the observations from electrophysiological recording, counterrolling eye movements and perceived tilt, that the otolith response path shows sensitivity to both acceleration and jerk. There is, of course, some ambiguity in interpretation of lateral otolith responses in terms of lateral acceleration or rotation about the roll axis. This ambiguity is normally resolved centrally by visual cues or semicircular canal responses to rotation. It can, on occasion, result in misleading illusions, such as the pitchdown illusion when an aircraft decelerates.

A typical response of the model to a sudden lateral tilt of the head is shown in figure 5-3-4, in which it is seen that the perceived tilt angle decays to about 40 percent of the actual tilt.

The model of the otolith assumes that it is stimulated only by the specific force in its plane and that compressive forces normal to this plane have no effect. Each otolith axis, then, is represented by the following transfer function:

$$\frac{\text{perceived lateral acceleration, } \beta}{\text{lateral acceleration, } A} = \frac{d(s + nc)}{(s + c)\,(s + d)}$$

$$= \frac{\text{perceived tilt angle}}{\text{tilt angle with respect to earth}}$$

or in terms of otolith displacement with respect to its macula:

$$\frac{\text{otolith displacement, } \delta}{\text{lateral acceleration, } A} = \frac{d}{(s + c)\ (s + d)}$$

$$= \frac{\text{otolith displacement}}{\text{tilt angle with respect to earth}}$$

As in the case of the canals, values for the various transfer function coefficients have been determined for humans. Both the currently accepted nominal values and the extreme values which can be represented by the physical model are tabulated below:

Table 5-3-2 Otolith Transfer Function Coefficients

	Nominal	Min.	Max.	Parameter
c	0.19	0.05	1.0	low freq. break, rad/sec
d	1.5	1.0	10.0	high freq. break, rad/sec
n	0.4	0	0.9	static gain

The significance of the parameters can be seen easily with respect to the step response of figure 5-3-4. Increasing d causes the response to rise more rapidly (with a time constant 1/d sec). Increasing c causes the response to decay toward its final value more rapidly (with a time constant 1/c sec).

Increasing n toward 1 results in a steady-state value to a step input which approaches the peak value and thereby reduces the adaptation effect.

Physical Analog of Vestibular System

As previously noted, the system consists of two major functional subsystems: the gimbal assembly, from which electrical signals representative of actual head motions are derived, and the computer and control console, which processes these signals in accordance with the preprogrammed mathematical models.

As shown in the functional block diagram of figure 5-3-5, each axis of the gimbal system is driven by an internal servo system in order to permit stimulation of head movement (7). Motion about each axis is controlled from the computer console. Appropriate front panel potentiometers, as well as suitable switches, plugs and jacks, have been provided for the insertion and control of both driving signals from external signal generators and generation of fixed signals for positioning of each axis.

The gimbal system motions, as specified in table 5-3-3, are capable of simulating all but the most violent head movements.

The innermost gimbal carries the inner package of nine inertial sensors, as shown in figure 5-3-6. A rate gyro package consists of three orthogonal instruments each with 1000°/sec full scale rating and resolution of 1°/sec. The miniature accelerometers are divided into two sets of three orthogonal instruments, located on the lateral axis and spaced by the distance between the ears. To simulate

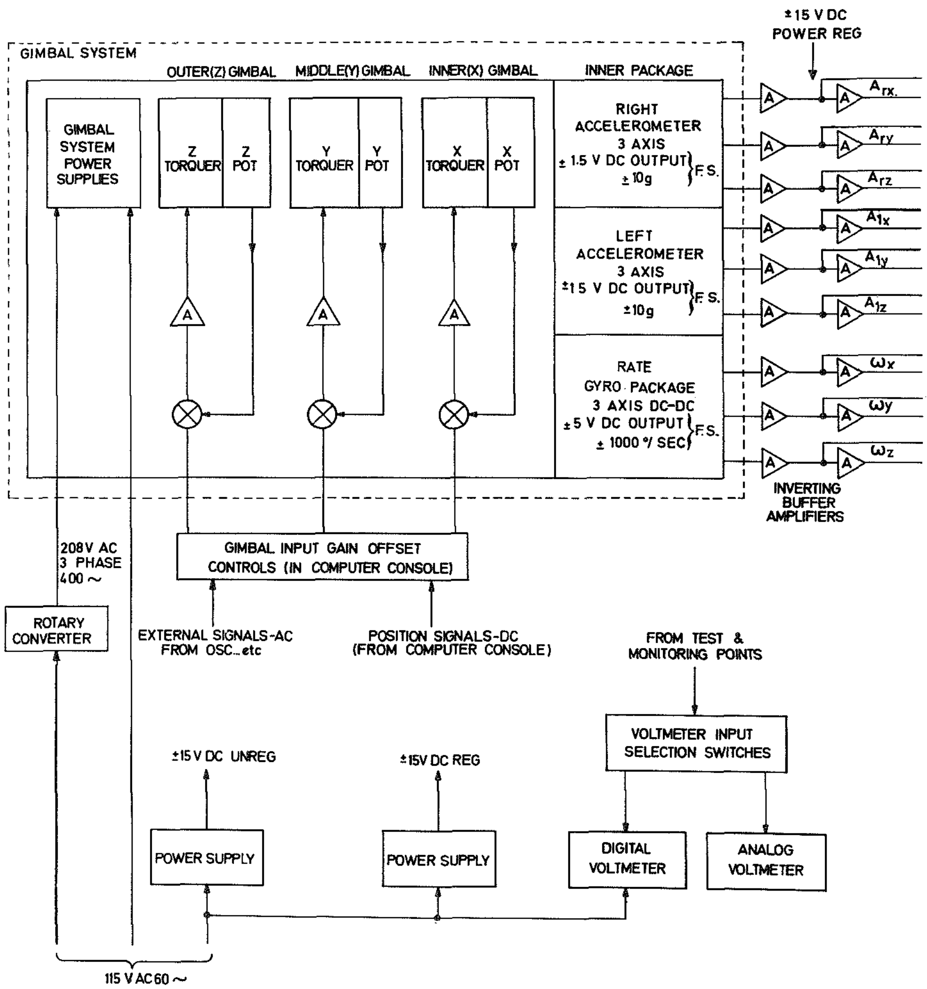

Fig. 5-3-5a Head motion simulator and inner package

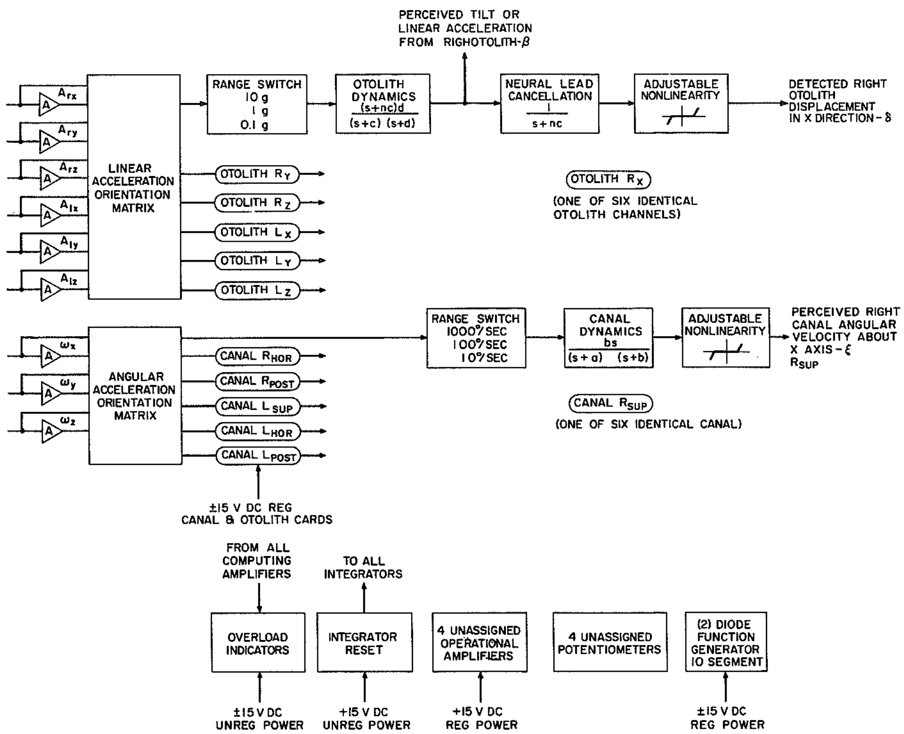

Fig. 5-3-5b Vestibular dynamics and nonlinear simulation

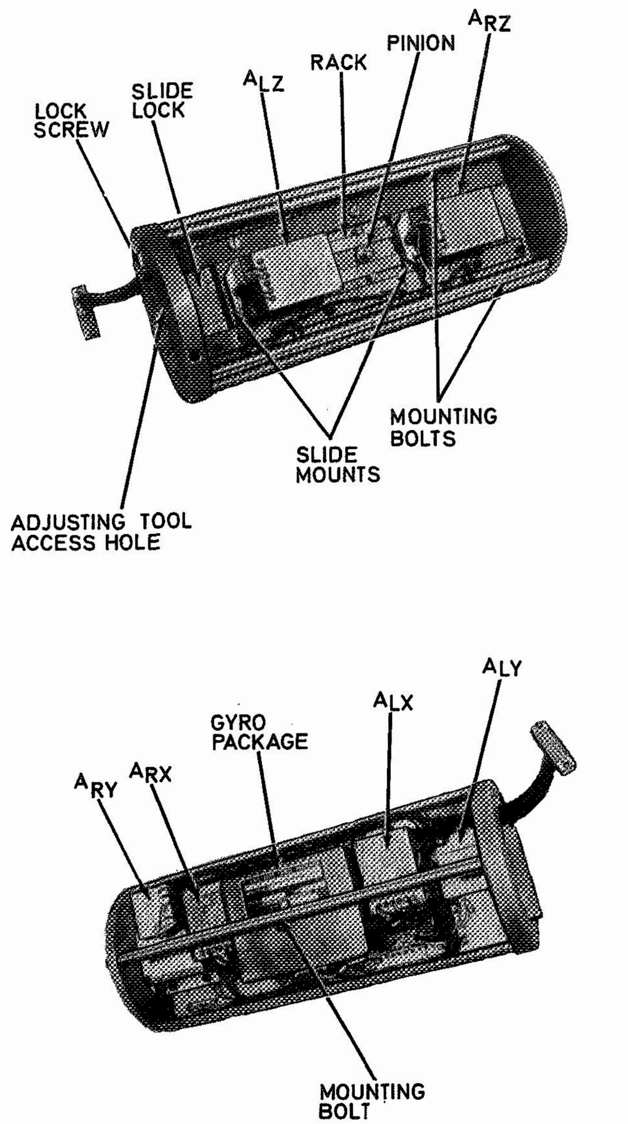

Fig. 5-3-6 Inner package showing gyros and accelerometers

Table 5-3-3 Specifications of Head Motion Simulator (fs = full scale)

	Axis		
	Roll Inner (X)	Pitch Middle (Y)	Yaw Outer (Z)
Bandwidth (-3db)	0.98 cps	0.90 cps	0.63 cps
Measured Max. Velocity	$\approx$200°/sec	$\approx$ 200°/sec	$\approx$ 200°/sec
Measured Max. Accel.	375°/sec^2	300°/sec^2	240°/sec^2
Maximum Displacement	±45°	±170°	±170°
Accuracy	0.5% fs	0.3% fs	0.3% fs

differences in head geometry, the inter-ear distance is adjustable. The distance between A_{LZ} and A_{RZ} accelerometers, left and right ear pitch axis respectively, is adjustable by a rack and pinion mount set from outside the system. The nominal inter-ear distance is 6.0 inches, with range of adjustment from 3.5 to 7.0 inches. The accelerometers have a range of 10 g's and resolution of 10^{-4} g. DC outputs from the nine motion transducers on the inner package are fed to the bank of buffer amplifiers in the computer console and from there to the two separate orientation matrices, one for otoliths (accelerometer signals) and one for canals (rate gyro signals). The orientation matrices, physically realized by cards of potentiometers, correspond to arrays of direction cosines independently relating the sensitive axis of each canal or otolith channel to the head axes.

Signals derived from the orientation matrices are then processed by the six canal and six otolith channels in accordance with the mathematical models as shown in figure 5-3-5b. Each of the canal channels and otolith channels processes data independently so that the characteristic time constants, scaling and nonlinearity factors are separately controlled by panel-mounted potentiometers. A three-position range switch is provided at the input to each channel, allowing for a scale selection which permits either gross phenomena or threshold effects to be studied. The output of each channel is fed through an adjustable simple nonlinearity. These devices make it possible to set independent values of perception threshold in each channel, if so desired. In addition, two unassigned, 10-segment diode function generators are provided to allow the effect of more complex nonlinearities to be studied.

The canal outputs are all related to perceived angular velocity, ξ. The otolith outputs are available both as otolith displacement, δ, and as perceived tilt or linear acceleration, β. Furthermore, the "neural lead cancellation" circuit can be modified by means of a panel-mounted switch, to function as a pure integrator. In this case, the output of that otolith channel represents perceived linear velocity.

The mathematical analogs are realized by operational amplifiers on printed circuit cards. The arrangement of the models and access to intermediate tie points is presented to the operator on front panels. The otolith model panel and the set of parameter adjustments available for each channel are shown in figures 5-3-7 and 5-3-8.

The primary outputs of the physical model are twelve real-time voltage signals which represent the outputs of each canal and each axis of otolith for the two ears. In addition, each of these quantities or any variety of intermediate points may be observed on the analog or digital voltmeter through selection switches shown in figure 5-3-9.

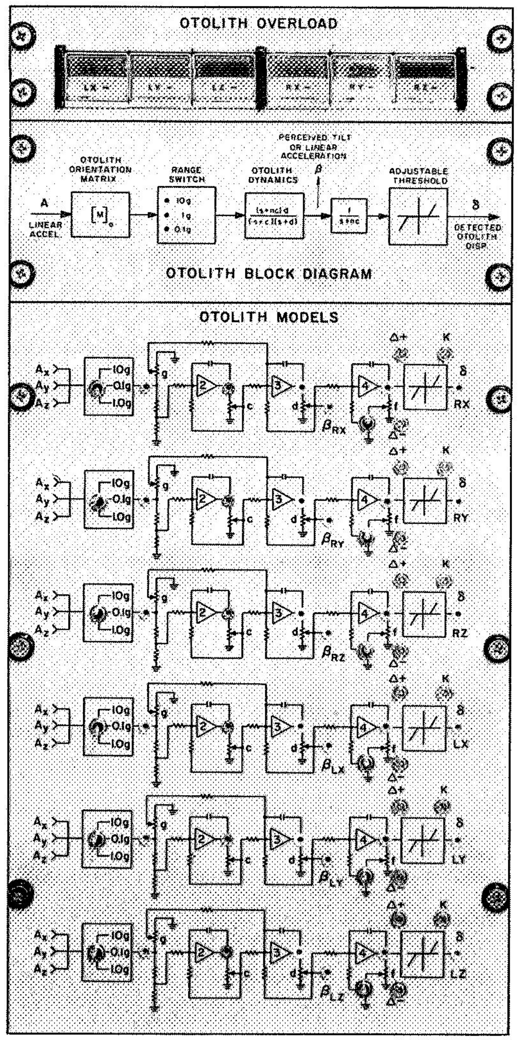

Fig. 5-3-7 Otolith model console panel

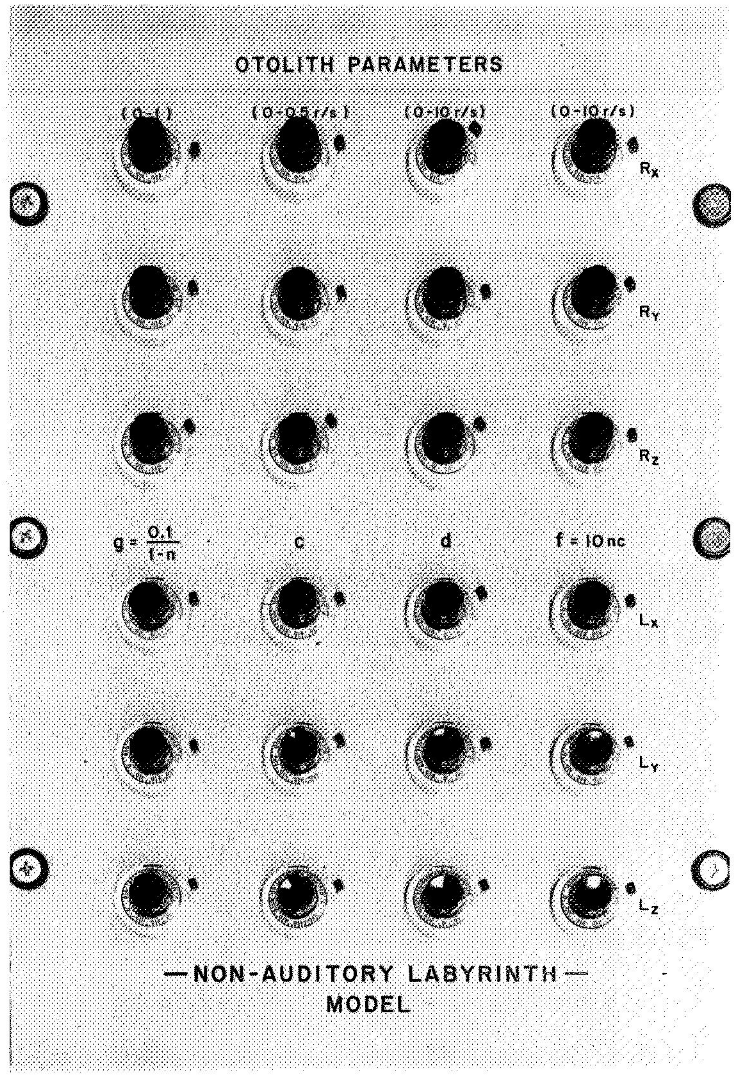

Fig. 5-3-8 Otolith model parameter adjustments

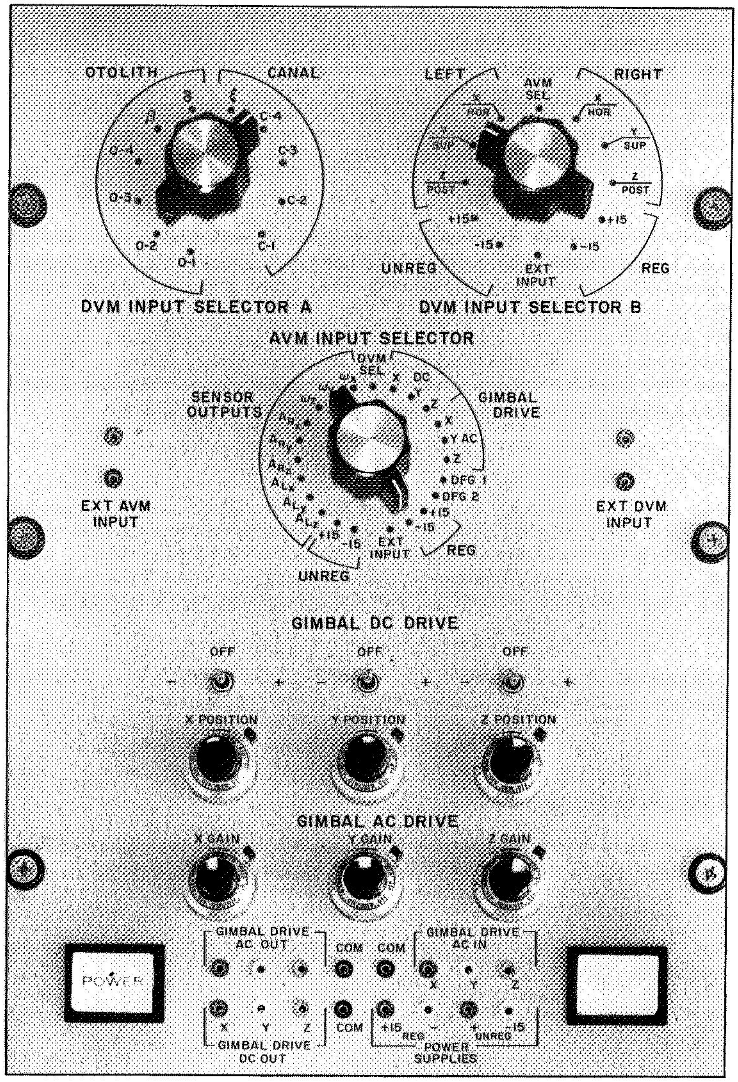

Fig. 5-3-9 Vestibular console controls

Conclusions

A first functional analog of the human vestibular system has been built, based on current mathematical models. It can be used to investigate the implications of these models in detail for a wide variety of inputs, before considering further experiments with humans. As discrepancies between detailed model responses and experimental data come forth, the models can easily be refined and extended. We have already begun experiments at M.I.T. with a type of "anti-vertigo" display which depends upon a model of the human vestibular system, subject to actual vehicle motions, to drive the display unit.

Acknowledgements

The mathematical models of the vestibular system were developed in the Man-Vehicle Lab., M.I.T., under support from the National Aeronautics and Space Administration, Grants NsG-577 and NGL 22-009-156. The physical model was built by the Biosystems Division, Space Sciences, Inc., Waltham, Massachusetts, under contract AF 33(615)-5038 for the Biodynamics and Bionics Division, Aerospace Medical Research Lab., Wright-Patterson Air Force Base, Ohio. The project engineer was Mr. Joel S. Newman and technical supervision from the Air Force was provided by Dr. Henning von Gierke and Dr. C. Stanley Harris.

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Discussion

R. von Baumgarten, University of Michigan. The otolith system was built in Evolution to counteract gravity. The otolith reflexes lead to movements of the body which are directed against the direction of otolith displacement. If otolith reflexes would contribute to stabilization against inertial forces, they should be directed the opposite way, which is not the case.

L. Young. In a "one-g" environment, because of the location of the otolith in the head, the postural reflex to return the head and the body to the vertical from some small displacement angle θ, by rotating about the ankle, produces two forces on the otolith: $m\theta g$ and $m\ell\ddot{\theta}$, where:

m = mass of otolith
θ = angular deflection of head from vertical (radians)
g = gravitational acceleration
ℓ = distance from otoliths to center of rotation of head (neck or ankles)

The system is not unstable for two reasons:

1) Because of the limited muscle strength and high moment of inertia of the head and body, $m\ell\ddot{\theta}$ is generally much smaller than $m\theta g$ except for very small angles (which might account for the observed postural limit cycles).

2) The righting reflex is probably not a continuous linear feedback system but rather a discrete system in which preprogrammed acceleration-deceleration commands (with zero average acceleration) are initiated and new samples taken only after completion of the basic righting response.

W.K. Taylor, University College, London. Is it necessary for the vestibular system to give exactly the same nerve impulse patterns under specific conditions throughout life? In other words do the organs contain a stable reference? If not, it may be possible to correct drift by a slow learning process or drift corrector, in which the differential action of postural stretch receptors act as a stable reference, that is in effect gravity itself acting on a vertical rod. The leaning of this can be detected by a pair of differential stretch receptors acting as a null device, in which common-mode changes of sensitivity are cancelled.

L. Young. Dr. Taylor's question relates to a very important area of vestibular research, and one which we are actively pursuing. Vestibular responses are changed by adaptation and by habituation. Some of the disturbing inconsistencies in the conventional semicircular canal model have been explained by our recent model for adaptation to prolonged angular acceleration (see Young and Oman in the Fourth Symposium on the Role of the Vestibular Organs in the Exploration of Space, Pensacola, Florida, September 1968.) This model represents the differential adaptation time courses of nystagmus and subjective orientation by separate first order filters, which update the cupula reference level on the basis of average cupula displacement.

Habituation to any specific vestibular stimulation which occurs repeatedly, or to a variety of movements in an unusual environment, has been observed but not explained. The problem is of considerable practical interest in prolonged weightlessness, rotating spacecraft (with associated Coriolis stimulation) and walking on the moon or other planets. Habituation has been demonstrated repeatedly, for example, after some days of living on the Slow Rotating Room at Pensacola.

The mechanism of habituation remains unknown. The vestibular reference is surely changed - perhaps to reduce the extent of visual-vestibular conflict or possibly to eliminate the frequency of inappropriate postural reflexes. The "inverted pendulum" postural reflex is one such possibility.